

The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding

Simon Verhulst^{1,*} and Jan-Åke Nilsson²

¹*Behavioural Biology, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands*

²*Department of Animal Ecology, Lund University, 223 62 Lund, Sweden*

Reproductive success usually declines in the course of the season, which may be a direct effect of breeding time, an effect of quality (individuals with high phenotypic or environmental quality breeding early), or a combination of the two. Being able to distinguish between these possibilities is crucial when trying to understand individual variation in annual routines, for instance when to breed, moult and migrate. We review experiments with free-living birds performed to distinguish between the 'timing' and 'quality' hypothesis. 'Clean' manipulation of breeding time seems impossible, and we therefore discuss strong and weak points of different manipulation techniques. We find that the qualitative results were independent of manipulation technique (inducing replacement clutches versus cross-fostering early and late clutches). Given that the two techniques differ strongly in demands made on the birds, this suggests that potential experimental biases are limited. Overall, the evidence indicated that date and quality are both important, depending on fitness component and species, although evidence for the date hypothesis was found more frequently. We expected both effects to be prevalent, since only if date *per se* is important, does an incentive exist for high-quality birds to breed early. We discuss mechanisms mediating the seasonal decline in reproductive success, and distinguish between effects of absolute date and relative date, for instance timing relative to seasonal environmental fluctuations or conspecifics. The latter is important at least in some cases, suggesting that the optimal breeding time may be frequency dependent, but this has been little studied. A recurring pattern among cross-fostering studies was that delay experiments provided evidence for the quality hypothesis, while advance experiments provided evidence for the date hypothesis. This indicates that late pairs are constrained from producing a clutch earlier in the season, presumably by the fitness costs this would entail. This provides us with a paradox: evidence for the date hypothesis leads us to conclude that quality is important for the ability to breed early.

Keywords: lay date; hatch date; clutch size; life-history evolution

1. INTRODUCTION

For birds and other organisms living in seasonal environments, the timing (laying date) and intensity of reproduction (clutch size) are two key decisions in the annual cycle in the sense that these traits are often strongly associated with fitness (Daan & Tinbergen 1997; Houston & McNamara 1999). Of these two decisions, selection pressures on clutch size have a long history of being studied experimentally, and the consequences for parents and offspring of rearing different numbers of young are relatively well known (Dijkstra *et al.* 1990; Vanderwerf 1992). However, decisions regarding laying date and clutch size are closely related, since the number of young that can be reared with a given effort depends on the timing of reproduction when, for example, food availability varies seasonally, and indeed clutch size typically varies with laying date (Klomp 1970). This raises the question as to what extent clutch size variation can be understood independently of an understanding of the effect of reproductive timing.

The fitness consequences of variation in timing of reproduction have been described extensively since the seminal paper by Perrins (1970), and on the descriptive level (as opposed to the experimental level), we therefore have good knowledge of seasonal patterns in reproductive success. However, the causes of these seasonal patterns are not well understood, since the effects of the actual timing of breeding are confounded with quality. Thus, the seasonal pattern in reproductive success may either be a consequence of timing *per se* (the date hypothesis), affecting all individuals in the same way, or reflect quality differences between breeders, irrespective of the timing of breeding (the quality hypothesis). 'Quality' as a cause of variation in reproductive success, as used here, will refer to the phenotypic quality or condition of the breeding individuals, the quality of their territories or other aspects of the environment, or any combination of these. For example, early-breeding females may breed on territories that are rich in food (Daan *et al.* 1990) or have a mate with more elaborate sexual signals which often induces a higher reproductive effort (Sheldon 2000) or be in better physiological condition (Moreno *et al.* 1998; Bearhop *et al.* 1999). Since birds breeding on high-quality territories or those in particularly good condition are likely to have higher reproductive success

* Author for correspondence (s.verhulst@rug.nl).

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independent of breeding time (Nilsson & Svensson 1993), it is not obvious to what extent seasonal variation in reproductive success can be attributed to timing effects *per se* as opposed to effects of quality. This is unfortunate, because when considering optimal breeding time we are primarily interested in the ultimate consequences of altering breeding time for the average individual (Baker 1938; Cuthill 2005). Thus, there is a need for experiments to disentangle the contributions of variation in time and quality to natural seasonal trends in reproductive success and other fitness components, to thereby obtain an unbiased estimate of the fitness consequences of breeding time (i.e. not biased by difference in quality between early and late breeders). Such knowledge is of particular importance in the light of global climate change and the interpretation and prediction of the effects this may have on (avian) populations (Both & Visser 2001). With a few pioneering exceptions, the experimental analysis of the fitness consequences of laying date started relatively recently, in the 1990s. In this paper, we aim to provide an overview of the experimental analyses of the fitness consequences of variation in time of breeding using birds as a model system. More specifically, we address the question as to what extent seasonal variation in fitness components can be attributed to effects of time, quality or a combination of the two. Our perspective in this paper is explicitly phenotypic, in the sense that the timing experiments we describe aim to estimate the fitness consequences of phenotypic variation in breeding time for the mean genotype.

Designing the perfect experiment, in which only the focal trait is manipulated, is difficult for most traits, but seemingly impossible for manipulations of breeding time. The problem is that we have no direct control over the timing of reproduction, and consequently can only manipulate timing indirectly. This introduces the problem that timing manipulations potentially also have effects on other traits (such as condition), and the effects attributed to manipulated timing may equally be attributed to other traits that were inadvertently manipulated. We therefore start with an overview of the experimental techniques to manipulate breeding time that are known to us, and the advantages and disadvantages associated with the different methods (table 1). This is followed by an overview of the results (table 2), where we try to draw general conclusions regarding the importance of time and quality in causing seasonal variation in reproductive success and other fitness components. Figure 1 provides a schematic overview of the possible outcomes of timing manipulations, and what can be concluded regarding the importance of timing and quality for different outcomes.

2. EXPERIMENTAL TECHNIQUES

(a) *Inducing replacement clutches*

In many species, removal of a clutch induces the pairs to produce a replacement clutch, thereby creating an artificially delayed group of breeding birds. The reproductive decisions (such as clutch size) and success of these pairs can be compared with a late control group (LC) composed of pairs with a natural late hatching date matching the actual hatching date of experimental

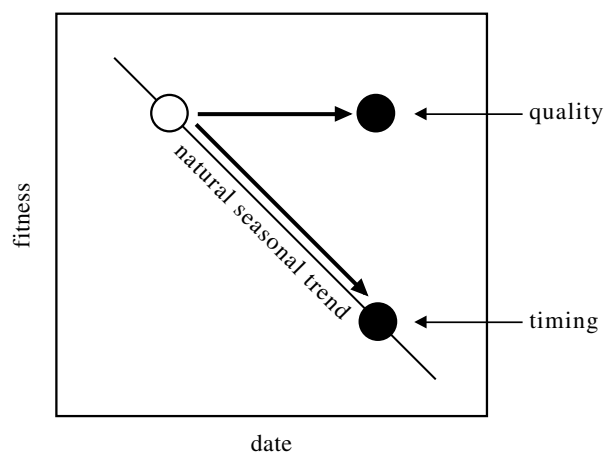


Figure 1. Schematic of timing experiments (delay only) and the interpretation of results. Fitness components can be compared between the EC group (EC; open dot) and the delayed group (filled dots), yielding information on the effect of timing. The delayed group can further be compared with pairs breeding at the same time (natural seasonal trend, or LCs), yielding information on the effect of quality. When the delayed group has a performance that is lower than the ECs, this provides evidence for a direct timing effect. When the delayed group has a performance that is higher than the performance of birds breeding late naturally, this provides evidence for an effect of quality. Note that the performance of the delayed group may be intermediate to the two possible outcomes shown, providing evidence for a mixture of effects of time and quality. (figure reproduced from Verhulst *et al.* 1995.)

pairs (figure 1). A variant of this technique is to remove a clutch to induce a replacement clutch as above but fostering the removed clutch to a pair with identical (early) expected hatching date, letting that pair rear the removed clutch and use it as an early control (EC; De Neve *et al.* 2004). This procedure has the advantage of allowing a paired comparison between early- and late-hatched broods with (on average) the same genetic background, but has the disadvantage that delayed pairs rear their own young while ECs rear foster young. A general advantage of inducing replacement clutches is that birds have the opportunity to adjust, for example, nest characteristics, clutch size and egg traits to the new time of breeding, allowing an experimental analysis of the effect of time of breeding on these traits. A further advantage is that the manipulation of timing is relatively large, compared with cross-fostering early and late clutches (§2b). There are two obvious disadvantages of this method. Firstly, in addition to being forced to breed late, pairs have produced the first clutch and the fitness costs of producing an extra clutch may not be negligible (Monaghan & Nager 1997; Visser & Lessells 2001). Secondly, this technique allows one to delay breeding, but yields no information on the fitness consequences of breeding earlier.

One risk associated with this manipulation is that the pairs that produce a replacement clutch are a non-random sample of the population, in the sense that pairs that produce a replacement clutch may differ in quality from those that do not. Such an effect could occur in either direction. Birds of high quality may be more likely to produce a replacement clutch because they are better able to cope with the added costs or can expect larger benefits. Alternatively, birds of high

quality may be maximizing fitness by not producing a replacement clutch when refraining from breeding increases the likelihood that they survive to breed another year while low-quality breeders may have low survival probability even when they refrain from breeding. Whatever the direction of the effect, it would bias the comparison between the delayed birds and both the EC group and the naturally late-breeding birds. There is no real solution to this problem, but one can reasonably assume that such biases will be limited when a high proportion of experimental pairs start a replacement clutch. When a non-negligible proportion of pairs refrain from starting a replacement clutch, one can estimate to what extent selection on phenotypic quality occurred, comparing e.g. lay date, clutch size and other parameters of the removed clutches between pairs with and without a replacement clutch (Verhulst & Tinbergen 1991).

(b) *Cross-fostering clutches*

This technique consists of cross-fostering clutches that differ in their expected hatching date, thereby manipulating hatching date and consequently the time when pairs have young in their nest. As with the induction of replacement clutches, reproductive success and other fitness components can then, for example, be compared between delayed pairs and pairs breeding late naturally (LC), and also with the EC pairs (figure 1). An advantage of this method is that the hatching date can be manipulated both forward and backward in time. The main disadvantage of this method is that timing is manipulated through a manipulation of incubation effort. When incubation is costly in terms of fitness (de Heij *et al.* 2006), and there is a linear decline in reproductive success, experimental effects are equally likely to be caused by the change in incubation effort as by the change in hatching date, as they are perfectly correlated. If however the seasonal trend in reproductive success is not linear, e.g. quadratic, it becomes possible to separate effects of timing and incubation duration (e.g. Brinkhof *et al.* 1993).

Further disadvantages of this method are that the scope for manipulation can be small when breeding time is highly synchronized and, linked to this, that manipulations are only possible within the naturally occurring reproductive window. Both disadvantages can, in principle, be overcome by cross-fostering clutches with other populations with earlier or later breeding seasons, but such experiments, to our knowledge, have not yet been carried out. One aspect of this manipulation that can be either an advantage or a disadvantage, depending on the details of the question asked, is that a natural shift in breeding time would often be accompanied by a change in clutch size, while normally clutches with similar number of eggs are exchanged (but see Wiggins *et al.* 1998). This can introduce a bias, in particular, when there is a steep seasonal decline in clutch size, because it will entail that for practical reasons, relatively small clutches for the time of year will be delayed, while relatively large clutches will be advanced. Note however that this can be resolved by combining eggs from different clutches. Another disadvantage is that hatching date is shifted from the perspective of the parents, but not from the

perspective of the clutch. If seasonal variation in reproductive success is caused (in part) by seasonal variation in egg characteristics, one could erroneously conclude that there is evidence for a causal effect of time of breeding, while it is in fact due to egg characteristics whose association with breeding date has not been broken by the experiment. Such a scenario is not unlikely, because evidence is increasing that there are long-lasting effects of egg composition on offspring performance (Schwabl 1993; Heeb *et al.* 1998; Crews & Groothuis 2005).

(c) *Other techniques*

(i) *Feeding until laying*

It is well established that supplementary feeding advances the start of reproduction in many species (Daan *et al.* 1989). Thus, in this way, birds can be tricked into breeding at a time when they would not normally have started reproduction, and if feeding is stopped after the start of laying or soon thereafter, this can be interpreted as a timing manipulation (Nilsson 1994). An important advantage of this method is that breeding time can be shifted to before the time that birds start breeding naturally. A disadvantage is that there may be carry-over effects of the extra food on the condition of the parents, in the sense that reproductive performance of the experimental birds may be higher as a consequence of the supplementary food, even when they were only fed up to the start of laying. A further disadvantage is that birds may have adjusted not only the laying date to the (over)estimated food availability, but also other traits such as the quality and number of eggs (Nilsson 1991). Consequently, the reproductive performance that is measured may not be an unbiased estimate of the reproductive performance achieved, had the birds started laying earlier without the misleading information.

(ii) *Storing eggs*

It is well known that it is possible to temporarily arrest the development of avian embryos by storing freshly laid eggs at low temperature. When the pair is given substitute eggs to ensure the clutch is not deserted, the original eggs can be returned to the nest at a later date to be incubated to hatching, creating an experimental delay of the hatching date. In many ways, the advantages and disadvantages of this manipulation are similar to those of the cross-foster manipulations (and we have categorized them as such in table 2), except that this manipulation yields delayed hatching dates, but no advanced hatching dates. An advantage of this manipulation is that eggs hatch in the environment they were potentially adapted to with respect to egg traits, such as concentrations of immunoglobulins and hormones, insofar as the adjustments made were independent of temporal variation on the time scale of the manipulation. A further advantage of this manipulation, in particular for populations in which breeding is highly synchronized, is that the hatching date can be delayed for a longer period than would have been possible with cross-fostering early and late clutches. One disadvantage of this manipulation is that temporary storage at low temperature may reduce hatching success (Wiggins *et al.* 1998), which may be

Table 1. Techniques to manipulate time of breeding. The column labelled 'direction' indicates whether the technique advances (–) or delays (+) breeding time (or both: –/+).

manipulation technique	direction	short description	potential inadvertent effect
inducing replacement clutches	+	remove clutch and treat replacement clutch as delayed clutch	production of first clutch which may affect condition
cross-fostering clutches	–/+	exchange clutches that differ in expected hatching date	modified duration of incubation which may affect condition
supplementary feeding	–	provide food to advance laying until laying has started	potential effects on condition
storing eggs	+	store eggs to arrest embryonic development and return to nest later	potential effects on egg quality + modified incubation duration
hold and release	+	hold birds to release later, to delay arrival or dispersal date	effects on condition
photoperiod manipulations	–/+	shift 'seasonal clock' through photoperiod manipulation	interpreting results difficult
endocrinological manipulations	–/+	shift 'seasonal clock' through hormonal manipulations	multiple effects of hormones complicates interpretation

indicative of a more general detrimental effect of the manipulation on the phenotypic quality of the embryo.

(iii) *Hold and release*

Timing of arrival can be manipulated by temporarily holding birds and releasing them at a later date. This approach can be applied, for example, to migratory birds, manipulating time of arrival on the breeding grounds (Cristol 1995), and to fledglings, manipulating the time when they join winter flocks (Nilsson 1990). A disadvantage of this method is that holding wild-caught birds in captivity is not always straightforward, making it difficult to rule out adverse effects on the phenotypic quality of the birds. One study that avoided this problem bred captive kestrels throughout the year through photoperiod manipulations, and released the fledglings at a fixed age, thereby obtaining information on their survival prospects throughout the year (Serge Daan 2006, personal communication). Although such an experiment is exciting, the information it yields on the fitness consequences of time of breeding is obviously limited to specific components, necessitating integration with other experimental information to complete the picture.

(iv) *Photoperiod manipulations*

Photoperiod plays a crucial role in the timing of birds' breeding seasons, since it determines the 'annual window' in which reproduction takes place (Meijer *et al.* 1990). Most of this paper deals with the ultimate factors shaping the time of breeding within this window. However, in theory, it should be possible to manipulate the photoperiod experienced by individuals using photo-manipulation (e.g. for birds roosting in nest boxes), thereby shifting the reproductive window. Insofar as the time of breeding is not determined by constraints such as energy availability, this could result in a shift of the time of breeding outside the normal reproductive window, which would be the main advantage of this manipulation. A potential disadvantage is that other reproductive decisions (e.g. clutch size, provisioning rate) may not be adjusted to the actual breeding time in the way it would have been, had the birds bred naturally at that date. For example, if

birds are manipulated into breeding before the normal breeding season, this implies that according to their 'seasonal clock', it is a later date than it is in reality. This may create a seasonal mismatch of other reproductive decisions (e.g. clutch size) reducing reproductive success compared with pairs breeding early spontaneously. Such effects could make the results of a photoperiod manipulation difficult to interpret.

(v) *Endocrinological manipulations*

Effects of photoperiod on breeding time are at least partly mediated by hormones (Deviche & Small 2002), and in theory, it should therefore be possible to manipulate breeding time through endocrinological manipulations. However, hormones often have many simultaneous effects, making it difficult to disentangle effects of breeding time from other endocrinological effects. Moreover, as for the photoperiod manipulations, other reproductive decisions may not be adjusted to the time of year in the way this would be done by birds breeding naturally at that date, further complicating the interpretation of the results.

3. RESULTS AND DISCUSSION

Many bird species show a consistent natural seasonal trend in reproductive success. Most of these relationships are either a linear decrease (the common pattern in species that fledge only one brood annually) or a pattern with an optimum in the middle of the season and then a steady decline (the common pattern in species that regularly fledge more than one brood annually). Thus, at least during the second part of the breeding season, early breeders seem to have a higher reproductive success than late ones. Such a seasonal trend would by itself predict high-quality parents or those breeding on high-quality territories to breed early, and so translate their phenotypic quality into high reproductive success. Independent evidence for this is the general finding that old individuals breed earlier than young ones (Perdeck & Cavé 1992; Moreno 1998). Older individuals are generally of higher phenotypic quality, either through individual improvement through experience, or through selective disappearance of low-quality individuals

Table 2. Results of studies that manipulated time of breeding through inducement of replacement clutches (R) or cross-fostering clutches differing in hatch date (CF). For the cross-fostering manipulations, effects of a delay (CF(D)) or an advancement (CF(A)) of hatching has been separated. For each fitness component, it is shown whether the authors concluded that there was evidence for the date hypothesis (D) or the quality hypothesis (Q), or both (D/Q). Indicated are also cases when synchrony or individual optimization best explained the results.

species	exp. R/CF	clutch size	growth rate	immunity	fledg. mass	fledg. success	prob. second clutch	local recruitment	references
herring gull	R	D				synchrony			Parsons (1975)
Cassin's auklet	R		Q						Morbey & Ydenberg (2000)
thick-billed murre	R		Q		Q				Hipfner (1997)
thick-billed murre	R				Q	Q			De Forest & Gaston (1996)
common guillemot	R					synchrony			Hatchwell (1991)
Brünnich's guillemot	R						Q		Hipfner <i>et al.</i> (1999)
black brant goose	R		D						Sedinger <i>et al.</i> (1997)
sooty tern	R					D			Feare (1976)
magpie	R					Q			De Neve <i>et al.</i> (2004)
starling	R	Q							Christians <i>et al.</i> (2001)
pied flycatchers	R				D	D			Siikamäki (1998)
great tit	(R)	D			D	D	D	D	Barba <i>et al.</i> (1995)
great tit	R	D/Q				Q	D	D	Verhulst <i>et al.</i> (1995)
great tit	R	D			D	D		D	Verhulst & Tinbergen (1991)
great tit	R	Q			D		D	D	Verboven & Visser (1998)
blue tit	R	D/Q							Nilsson (2000)
blue tit	R	D			D	D			Sanz (1999)
blue tit	R							D	Svensson (1997)
common tern	R		Q			D/Q			Arnold <i>et al.</i> (2004)
	CF(D)		D			D/Q			
	CF(A)		D			D			
shag	CF(D)					Q			Daunt <i>et al.</i> (1999)
	CF(A)					Q			
chinstrap pen-guin	CF(D)				D				Moreno <i>et al.</i> (1997)
	CF(A)				D				
greater snow goose	CF(D)		D						Lepage <i>et al.</i> (1999)
	CF(A)		D						
herring gull	CF(D)					Q			Brouwer <i>et al.</i> (1995)
	CF(A)					D			
coot	CF(D)					D			Brinkhof <i>et al.</i> (1993)
	CF(A)					D			
coot	CF(D)				Q				Brinkhof (1997)
	CF(A)				D				
coot	CF(D)						D		Brinkhof <i>et al.</i> (2002)
	CF(A)						D		
coot	CF(D)							Q	Brinkhof <i>et al.</i> (1997)
	CF(A)							D/Q	
tree swallow	CF(D)				Q				Wardrop & Ydenberg (2003)
	CF(A)				D				
great tit	CF(D)						D		Verboven & Verhulst (1996)
	CF(A)						D		
great tit	CF(D)			D					Dubiec & Cichon (2005)
	CF(A)			D					
blue tit	CF(D)							D	Norris (1993)
	CF(A)							D	
collared fly-catcher	CF(D)					D			Wiggins <i>et al.</i> (1994)
kestrel	CF(A)					ind. opt.			Aparicio (1998)
	CF(D)					ind. opt.			

(van de Pol & Verhulst 2006). Hence, correlations between age and breeding time indicate quality differences between early and late breeders. This raises the question as to what extent seasonal declines in reproductive success are attributable to date effects *per se*. It is not necessary to invoke a direct effect of date on reproductive success to predict high-quality birds to breed early, because the fitness benefits for high-quality breeders to reproduce early may be independent of the seasonal decline in reproductive success that is observed. Instead, the fitness benefits of early breeding may be found in components of the residual reproductive value of the parents, such as the probability of re-nesting within the same season, or survival of the parents after breeding. Given that there are *a priori* reasons to expect both time and quality to play a role, the value of timing experiments should be to identify situations when date (either absolute date or date in relation to other individuals in the population) contributes to the seasonal pattern in different fitness components.

(a) *Interpretation of the data*

(i) *Experimental biases*

Both the main experimental techniques to disentangle the relationship between quality and date, inducing replacement clutches and cross-fostering, suffer from unwanted side effects (table 1). The experimentally delayed hatching in cross-fostering manipulations is qualitatively the same as the delayed hatching induced by removing the first clutch, and the two techniques can thus be compared. By combining studies evaluating traits connected to reproductive success during the current breeding episode, i.e. nestling quality (growth rate, fledging mass and immunocompetence) and nestling survival (fledging success), we obtain a large enough sample to evaluate potential differences between the techniques. As can be seen in table 3, the distribution of studies supporting either the parental quality or the date hypotheses is similar for the two techniques. Thus, at least on this crude qualitative level, the two experimental designs that delay hatching date seem not to differ in their propensity to result in support for the two explanations, even though the induced extra parental effort differs between the experiments. This is not to say that the experiments are unproblematic when it comes to evaluation of the results (see Hansson *et al.* 2000), just that the potential bias of a prolonged incubation period seems to be equal to producing an extra clutch in relation to experimental outcomes.

(ii) *Current breeding episode*

Among the nine cross-fostering studies aimed at evaluating traits affecting the current breeding episode, four resulted in different conclusions between the delayed and the advanced parts of the experiment (table 2). In common terns *Sterna hirundo*, herring gulls *Larus argentatus*, European coots *Fulica atra* and tree swallows *Tachycineta bicolor*, early-breeding individuals that were experimentally delayed performed better than expected on the basis of the performance of late-breeding controls, showing that at least part of the seasonal decline could be explained by the parental quality hypothesis. However, the reciprocal manipulation, an experimental

Table 3. Number of studies resulting in quality (Q), date (D) or a combination of them (D/Q) as explanation for a seasonal decline in traits connected to the current breeding episode (growth rate, immunity, fledging mass and success in table 1) following an experimental delay of hatching date either by inducing pairs to re-lay or to cross-foster eggs with a later hatching date than the original one.

	Q	D	D/Q
induced re-laying	5	7	1
cross-fostering	4	5	1

advance of the hatching date, resulted in the breeding trait under consideration following the predictions from the date hypothesis (Brouwer *et al.* 1995; Brinkhof 1997; Wardrop & Ydenberg 2003; Arnold *et al.* 2004). Thus, early-breeding, high-quality pairs are able to at least partly compensate when faced with a delayed hatching date, whereas late-breeding, low-quality pairs for which the hatching date is advanced are able to attain the same high success as early breeders. This might depend on a reduction in the length of incubation, inherent in these kinds of experiments, making it possible for the advanced birds to be as successful as naturally early pairs during later breeding phases due to the saved part of the incubation effort. Another explanation might be that late breeders would have to pay a higher cost than early breeders to produce a clutch early in the season. Thus, under this scenario, the difference in quality between early and late breeders is expressed in the costs paid for breeding early, and not in their ability to rear a brood once it has hatched. The latter follows from the observation that when they obtain an early clutch for free, by the manipulation, they have the same success as early pairs. Egg laying and/or incubation may be a general constraint for late breeders, since eight out of the nine advancement experiments conformed to the predictions from the date hypothesis (table 2).

(iii) *Local recruitment*

Six out of seven studies that evaluated the seasonal decline in local recruitment supported the date hypothesis (table 2). However, the taxonomic bias is severe since all of these six studies were conducted on great (*Parus major*) or blue tits (*Cyaniste caeruleus*); the only study supporting the parental quality hypothesis was conducted on coots (Brinkhof *et al.* 1997). Even though the number of species studied is very limited, the results suggest that the mechanism responsible for this pattern is establishment success in dominance-structured social systems during the non-breeding season (Nilsson 1999). Such establishment is crucial for winter survival in these sedentary species. In an experimental study of factors potentially determining establishment success in another tit species, the marsh tit *Parus palustris*, it was found that the timing of prospecting for an establishment site was decisive for juvenile establishment success irrespective of body size and hatching date *per se* (Nilsson 1990). Furthermore, survival rate of great tits that fledged late in the season was enhanced in years when the number of birds that fledged early in the season was experimentally reduced (Verhulst 1992). Thus, the important factor explaining

the seasonal decline in local recruitment seems to be timing relative to other pairs rather than absolute timing during the breeding season. In line with the suggestion that relative timing is important during competition, juvenile coots (*Fulica atra*) do not spend the non-breeding season in a stable territorial system, and dominance advantages due to prior occupancy can be assumed to be of much less importance (Brinkhof *et al.* 1997). Instead, size may be important for survival among young coots. This also reveals a further bias in the dataset, since only resident species have been studied with respect to recruitment, and selection pressures may well differ between migratory and resident species.

(iv) *Residual reproductive value*

The seasonal decline in the probability of producing a second clutch is another reproductive trait for which the seasonal decline was generally causally related to date. Only one out of six studies suggested that parental quality was sufficient to explain the seasonal trend. Furthermore, this study on Brünnich's guillemots (*Uria lomvia*) did not deal with true second clutches (which are normally defined as clutches started after successfully rearing the first brood), but with the probability of re-laying following experimental egg removal (Hipfner *et al.* 1999). The reproductive decision to produce a second clutch is probably directly related to the length of the breeding season remaining when it is possible to produce a second clutch, which, in turn, is dependent on the expected fitness when breeding late (Verhulst *et al.* 1997). Breeders need to have enough time for moult and/or preparations for migration or winter acclimatization. The length of a breeding episode is rather constant with limited possibilities to speed it up (Kluyver *et al.* 1977), independent of the phenotypic quality of the pair or their territory. Thus, seasonal decline in this reproductive trait will be determined by date rather than by quality *per se*.

Residual reproductive value is also dependent on parental survival to the next breeding season. So what is the effect of timing manipulations on parent survival? In two manipulations where replacement clutches were induced, some limited support for increased mortality of manipulated females was found. In 1 out of 4 years, delayed great tit females had lower survival rates than control females (Verhulst *et al.* 1995), and in 1 out of 2 years, delayed female blue tits had reduced survival (Nilsson & Svensson 1996). Cross-fostering experiments have provided us with even more mixed results. In collared flycatchers (*Ficedula albicollis*), experimental delay negatively affected female survival (Wiggins *et al.* 1998), whereas in coots, delayed parents enjoyed higher survival than controls (Brinkhof *et al.* 2002). The studies resulting in some evidence for reduced survival of delayed females are all conducted on small, short-lived passerines. Having rather short life expectancy, individuals of such species may invest more in late breeding attempts than individuals of species with longer life expectancy. Thus, parents of small passerines, engaged in rearing a replacement brood, may invest more and suffer from increased reproductive costs, for example through reduced time for moulting, than parents in long-lived species. Such time constraints

may translate into increased mortality, in particular, during years with especially harsh winter conditions (Nilsson & Svensson 1996; Verhulst 1998). When breeding time has been experimentally advanced, the limited data that are available suggest that parents suffer higher mortality rates than controls (Nilsson 1994; Brinkhof *et al.* 2002). This indicates a cost to early breeding and that parents trade off this survival cost against current reproductive success, which is enhanced when breeding is advanced. Thus, depending on parental or territorial quality, individual parents will maximize fitness by finding the optimal solution to the trade-off between current and future reproductive success. In long-lived species with a different trade-off between survival and current reproductive success, advancement of breeding may result in reduced current reproductive success instead of reduced survival as found in European kestrels (*Falco tinnunculus*; Aparicio 1998; table 2).

(b) *Mechanisms underlying a seasonal deterioration of the environment*

When at least part of the seasonal decline in reproductive success can be attributed to date *per se*, the decline has to be due to some factor that deteriorates with season. This might be absolute date (reducing the time window for post-breeding activities), relative date (influencing social interactions), food availability and predation pressure. In addition to being interesting in its own right, understanding the mechanisms mediating the seasonal decline in reproductive success will be important in evaluating to what extent the observed effects can be attributed to the focal trait (timing of breeding), as opposed to an experimental bias introduced because clean manipulations of breeding time are not possible.

In seasonal environments, the length of the breeding season is constrained by necessary preparations for the non-breeding season. One such preparation is moult, i.e. the replacement of plumage. Species undergoing a complete moult after breeding are often time constrained as evidenced by an increasing breeding-moult overlap among late-breeding individuals (e.g. Svensson & Nilsson 1997). Furthermore, delayed moult has been associated with reduced survival (Nilsson & Svensson 1996; Siikamäki 1998) and reduced future reproductive success (Nilsson & Svensson 1996; Wiggins *et al.* 1998). Thus, such a trade-off between current reproduction and moult may result in reduced parental effort late during the breeding season, potentially explaining the negative relationship between traits connected with current reproduction and absolute date. Additionally, start of moult among offspring is closely related to hatching date (Bojarinova *et al.* 1999), potentially reducing the survival prospects of late-produced fledglings. Thus, absolute date can be important for both parents and offspring, simply because they may be running out of time.

There are two ways in which relative timing may be important. Firstly, it may simply be important to breed early relative to conspecifics or some seasonal change in the environment. The advantages for early-hatched fledglings have already been discussed in relation to the

seasonal decline in local recruitment. Besides the advantage of being early in competition over space due to prior occupancy (Nilsson 1989), early fledglings in species without a stable flock structure during the non-breeding season may also enjoy higher survival probabilities than late fledglings due to an increased experience in agonistic encounters with age (Arcese & Smith 1985). Secondly, it may be important to breed in synchrony with conspecifics or some seasonal change in the environment. Experimental manipulations of pairs that result in hatching dates, which deviate from that of the majority of pairs, will then result in reduced fledging success in both advanced and delayed situations (table 2). Several advantages of synchronous breeding have been proposed, e.g. improved defence, increased vigilance and dilution of predation pressure (Hatchwell 1991).

(v) *Food availability*

The classic example of timing relative to the seasonal environment is the timing of breeding seasons of great tits relative to the annual peak in caterpillar abundance (Perrins 1965; van Balen 1973; Verboven *et al.* 2001). For food availability to explain the seasonal decline in current reproductive success, a large proportion of the population should breed on the downward slope of caterpillar abundance. Among great tits, this seems to happen in the majority of years (Daan *et al.* 1989; Verboven *et al.* 2001). In an elegant experiment, Siikamäki (1998) provided supplemental food to experimentally delayed pied flycatchers (*Ficedula hypoleuca*). Whereas delayed birds suffered from reduced fledging success and lower fledging mass compared with EC birds (table 2), extra food restored their breeding success to the levels of the ECs. Thus, in this case, a seasonal decline in food availability seems to be responsible for the support of the date hypothesis. Similar conclusions were reached in a study of experimentally fed coots (Brinkhof & Cavé 1997). The proportion of pairs starting a second clutch may also be influenced by the seasonal variation in food availability as the frequency of second clutches among great tits has been shown to decrease with timing in relation to the caterpillar peak with little effect of absolute date (Verboven *et al.* 2001).

(vi) *Predation pressure*

If the risk of predation increases seasonally, this can explain a seasonal decline in fledging success and/or local recruitment. In some colonial species, predation from conspecifics may constitute a serious mortality risk among nestlings. The risk of cannibalism is lower for birds breeding early during the season. Such adults will have vulnerable young at a time when most other adults are incubating and not yet a serious threat (Hunt & Hunt 1976). Also post-fledging predation seems to increase with season. The rate of disappearance of great and coal tit (*Parus ater*) fledglings during their first two to three weeks outside the nest increased markedly with season (Naef-Daenzer *et al.* 2001). The majority of the disappeared fledglings were assumed to be taken by predators. In another study on the fate of ringed great tit fledglings, rings were searched for in nests of sparrowhawks, *Accipiter nisus*,

during the breeding season of great tits (Götmark 2002). Risk of predation also increased seasonally in this study. In both studies, it was concluded that a fairly large proportion of fledglings were taken by predators, thus potentially explaining some of the seasonal decline in local recruitment (table 2). Since large brood size (Götmark 2002) and low mass, especially late during the season (Naef-Daenzer *et al.* 2001), also increased the risk of predation, some of the seasonal decline in clutch size may be due to a trade-off between brood size and predation risk since fledgling mass decreases with increasing brood size. Potential reasons for the increased predation risk with season are connected with some of the other mechanisms. For example, a seasonal decline in food availability will result in late fledglings that beg more intensively and, consequently, are easier for predators to find (Götmark 2002). Alternatively, predators will time their reproduction to the peak abundance of fledglings usually following the fledging of the abundant migratory species. Since tits in general start to breed earlier than many migratory species, it would be advantageous for them to breed sufficiently early to, as far as possible, separate the timing of their own fledglings from the peak fledging in the environment. They will then avoid the time when predators have high food requirements due to nestling feeding (Götmark 2002).

(vii) *Parasites*

Nest parasites have the potential to affect nestling growth rate and fledging success (Richner *et al.* 1993). For nest parasites to explain the seasonal decline in current reproductive success, their effect should increase with season. However, in one of the most common nest parasites, the hen flea *Ceratophyllus gallinae*, this seems not to be the case since number of fleas did not vary with season in nests of either great tits (Heeb *et al.* 1996) or blue tits (Tripet & Richner 1999). Data on the seasonal development of other nest parasite populations are sparse. However, abundance of blowflies *Protocalliphora azurea*, a common nest parasite in certain areas, seems to increase with season (Merino & Potti 1995), and can thus potentially add to a seasonal decline in current reproductive success in areas where it is common.

(viii) *Parental investment*

What evidence is there for seasonal variation in parental investment and/or reproductive effort, and to what extent could such effects cause seasonal variation in reproductive success? The general result that birds produce fewer young later in the season cannot be taken as evidence for a decline in reproductive effort, since animals breeding in a poorer environment may have to invest the same effort for a lower result due to deterioration of the environment or because they breed in territories of lower quality (e.g. Daan *et al.* 1990). In line with this, reproductive effort measured as metabolic rate appears to be independent of the timing of reproduction (Verhulst & Tinbergen 2001). However, it is conceivable that, under certain circumstances, parental investment will decline with season. This would be possible if the trade-off between current and future reproduction changes during the season. Parents may, for example, start to moult during the later

part of the breeding season (Svensson & Nilsson 1997) or value their young less if they are produced late during the season (Daan *et al.* 1990). This may explain the seasonal decrease in feeding rate of female house sparrows, *Passer domesticus*, breeding in aviaries although food was provided *ad libitum* (Moreno-Rueda 2004).

4. CONCLUSIONS

Taken together, a large number of experimental studies of the fitness consequences of breeding time that have appeared in the last 15 years provide strong evidence for the importance of both timing and quality in causing the seasonal decline in reproductive success. The finding that both are important is in agreement with our *a priori* expectation (§3a). Although the number of studies that is now available is fairly large, only a minority followed offspring and parents for a year or more. Consequently, conclusions regarding the relative importance of time and quality are usually restricted to specific fitness components (table 2), and our knowledge is still limited concerning the relative contribution of time and quality to the seasonal decline of fitness prospects (but see Verhulst *et al.* 1995). The available dataset further suffers from a taxonomic bias, consisting largely of hole-breeding passerines and seabirds, although it is worth noting that the most comprehensive study to date was on a waterbird, the European coot (see Brinkhof *et al.* 2002, and references therein).

As discussed in §3b, there is compelling evidence indicating that the breeding time relative to conspecifics is of major importance, in particular for the survival prospects of independent offspring (at least for resident species). If relative timing is important, i.e. the optimal time of breeding depends on the time of breeding of conspecifics, this implies frequency-dependent selection on breeding time. Unfortunately, with respect to the proximate factors determining breeding time, the importance of the behaviour of conspecifics has to our knowledge been little studied so far. An exception is the study of Meijer & Langer (1995), who rationed the food of captive starlings (*Sturnus vulgaris*) which delayed the start of laying. Captive starlings housed next to the (late breeding) food-rationed birds delayed the start of laying compared with a control group that was isolated from the rationed birds, thereby increasing the breeding synchronization of the 'population'. This elegant experiment illustrates the potential importance of social factors in determining breeding time.

The studies discussed in this paper go some way towards providing a better understanding of the causes of seasonal variation in reproductive success, and hence the timing of breeding, but only on a relatively fine scale, since the breeding season is a more or less fixed window in the annual cycle, and data can only be collected within this window. One can however also ask questions about the time of breeding on a broader time scale, for instance, what would be the consequences for reproductive success and other fitness components if birds, for example, moulted in spring and bred afterwards instead of breeding before the moult (Barta *et al.* 2008)? Since direct empirical estimates will be almost impossible to obtain, another approach is required. One

potential solution is to use theoretical models that are based on an understanding of the mechanisms mediating seasonal variation in reproductive success to estimate the fitness consequences of alternative breeding times (Houston & McNamara 1999). On the other hand, such an approach can only work to the extent that one can assume that the environment, including, for example, the behaviour of predators and parasites, would not coevolve when birds change their breeding season. It is reasonable to assume that, for example, depredation of fledgling tits by sparrowhawks would be less if they fledged two months earlier, but it seems probable that such a change, especially if many potential prey species adopt the same reproductive timing, would elicit an evolutionary response in the time of breeding of the sparrowhawk, which is synchronized with the breeding seasons of their prey species (Newton 1979).

When reproductive success increases when hatching date is experimentally advanced, e.g. by cross-fostering early and late clutches, this raises the question why late pairs did not start breeding earlier in the first place. This was discussed previously by Perrins (1970), on the basis of correlational evidence, and the solution he suggested was that there were constraints that prevented birds from breeding on the date with which they would maximize their fitness. Alternatively, one can replace the concept of a constraint on breeding time with the view that the breeding time is the outcome of an optimization process, where optimal breeding time is determined by the combined fitness costs and benefits associated with breeding time. Assuming that the birds follow an optimal decision rule, in the sense that they start laying at the date that maximizes their fitness, this suggests that there are costs associated with early breeding which make it suboptimal for the late pairs to breed earlier than they do. This follows from the finding that the benefits (reproductive output) usually increase when breeding is experimentally advanced, and without invoking fitness costs of earlier laying, it is difficult to understand why late birds do not breed earlier than they do. Indeed, there is some evidence for fitness costs of early breeding (Nilsson 1994; Brown & Brown 2000). In a way, this indicates that early pairs are of higher quality, in the sense that they are better able to cope with the costs of laying early in the season. This introduces an interesting paradox: when the seasonal decline in reproductive success is attributed to timing *per se*, this indicates that early breeders are of higher quality! Note that according to this view, phenotypic quality is a multidimensional trait, with birds having different quality aspects that affect various life-history aspects (costs of breeding early, ability to rear a brood at a particular breeding time) separately and perhaps even independently.

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